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CHARLES MINOT AND THE HARVARD EMBRYOLOGICAL COLLECTION: OVER A CENTURY OF DEVELOPMENT

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Abstract. The Harvard Embryological Collection (HEC) is a prime example of a historic histological embryo collection. The HEC was started in the late 19th century by notable American anatomist Charles Sedgewick Minot. The collection is broadly systematic, including 60 taxa with at least several examples from every vertebrate class. It was founded in a collaborative spirit to provide the research community a "cyclopedia" to promote new research and provide reproducible staging in embryology. The collection was successful in spawning a number of seminal works in the field. Slides were prepared according to strict archival standards with the intention that HEC slides would act as permanent vouchers. However, the collection became dormant and unrecognized for most of the 20th century. The collection, now safely housed at the Museum of Comparative Zoology, is again available to researchers, and as its founders intended, it is still well preserved even after 100 years. It continues to serve as an archive for research of the early 20th century and it holds great value and promise to embryological research in the 21st.

INTRODUCTION

Many of the largest embryological collections today are the same collections that drove embryology research in the late 19th and early 20th centuries. Historic collections such as the Embryology Collection at the Hubrecht Laboratory in the Netherlands (Bangma, 1988; Richardson and Narraway, 1999), among several others (Carter, 2008), have all been recognized as significant resources for embryology. The Harvard Embryological Collection (HEC) of Charles Sedgewick Minot (1852–1914) is another broadly systematic embryo collection that had historic impact and now deserves renewed recognition.

Charles Sedgewick Minot and the HEC have gone relatively unnoticed since their worldwide recognition in the early 1900s. However, both have left substantial and well-deserved legacies. Minot was a leading embryologist and was, "by common consent" among his peers, the foremost American anatomist of his time (Lewis, 1916). He studied briefly under Louis Agassiz at the Museum of Comparative Zoology (MCZ)

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and later under the leading European embryologists of his day. This training no doubt influenced his collection-based approach to comparative embryology. This approach culminated in Minot's founding of the HEC. The collection grew to worldwide prominence and was respected as a valuable contribution to science (Mall, 1913). Minot's death and the decline of descriptive embryology in the early 20th century, however, left both his legacy and the HEC in obscurity. The collection is now held at the MCZ and is again available to researchers.

The current paper reviews the history of the collection and offers a profile of its holdings to document the HEC's full extent. The general methods and materials used to construct the collection are outlined. Additionally, the potential for slide digitization and three-dimensional (3D) reconstruction is discussed. The breadth and depth of the collection combined with the potential for renewed study using modern imaging methods mean that the HEC is not only one of the great embryology collections historically but also a valuable resource for future research.

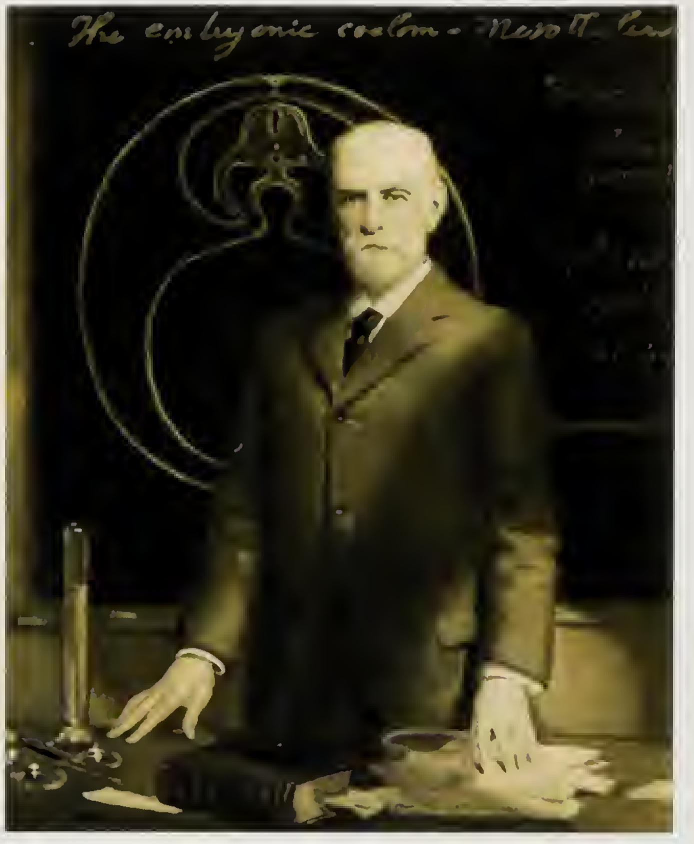

Figure 1. Charles Sedgwick Minot (1852–1914). Artist: Charles Sydney Hopkinson. Credit: Harvard Art Museums/Fogg Museum, Harvard University Portrait Collection, Gift by subscription of friends of Charles Sedgwick Minot, Harvard Medical School, H510. © President and Fellows of Harvard College

CHARLES S. MINOT AND THE HEC

Charles Sedgewick Minot (Fig. 1) was Professor of Comparative Anatomy at the Harvard University Medical School from 1892 until his death in 1914. Minot may have been a medical doctor by training and profession but his broad, comparative approach to anatomy and embryology across animal diversity led colleagues to occasionally view him as more of a zoologist than a physician. He received his Bachelor of Science from Massachusctts Institute of Technology and then entered the natural history program at the MCZ at Harvard, led at that time by Louis Agassiz (Lewis, 1916). Minot has been remembered as one of Agassiz's last students and as a part of his teaching legacy (Lewis, 1916; Morse, 1920; Jordan, 1923).

However, Minot's time at the Museum with Agassiz was brief and he exited the natural history program early (Morse, 1920). He moved to the Harvard Medical School and would also study extensively in Europe under leading anatomists, including Carl Ludwig, Wilhclm His, and Karl Ernst von Baer (Lewis, 1916). This time was formative for Minot's work, with most of his publications during this period focused on histological technique and embryology. Minot became a user and admirer of the Wilhelm His embryology collection, which he would specially acknowledge later in his career (Minot, 1892). Aftcr his graduation from Harvard Medical School in 1878, Minot was eventually appointed lecturer of embryology at the School, although with reservations as so much of his earlier work had focused on zoology and comparative embryology and not directly on medicine (Lewis, 1916).

Minot's early MCZ experience seemingly followed him to Harvard Medical School. Although he used embryology to build his career as a medical lecturer, he regularly ventured into comparative research on non-human subjects, such as guinea pig embryos. Even though Minot received collegial reminders that his first duty was to train medical professionals, he remained adamant that studying embryology should enable students to better understand anatomy (Morse, 1920). His approach proved successful and he advanced within the Medical School to eventually earn full professorship after publishing his landmark text, *Human Embryology*. This happened to be one of his last publications on human anatomy. Shortly thereafter, he revitalized his efforts in comparative embryology by formally announcing his plans to build the "Harvard Embryological Collection" (Minot 1900). The collection would include human embryos; however, its massive and diverse holdings distinctly resembled a systematic zoological collection.

HISTORY OF THE HEC

Minot built his embryology collection in the same spirit as a natural history collection. He saw the HEC as a "cyclopedia of vertebrate embryology to which one can turn at any time and get the desired information as to the principal features of development of any structure whatsoever" (Minot, 1905). The concept likely grew from his appreciation for the European embryology collections he visited as a student and also from Agassiz's influence early in his career. Minot even went so far as to compare his collection to zoological types in systematic literature. He thought that his slide series could be the lasting exemplars by which developmental stages were defined.

The size and scope of the HEC has long been underestimated. Minot's last published report (1905) listed 937 series from 28 different taxa; however, the collection was far from complete at that time. When inventoried in 1976, the HEC held 2,535 series of paraffin-embedded, stained, and sectioned embryos and an estimated 32,000 individual slides (Williston, 2010). Although the collection is large in terms of total slide series, the HEC includes only 61 species, a limited diversity when compared with similar embryo collections (see Table 1). The Hubrecht Institute Embryo Collection, for example, represents 600 vertebrate species (Bangma, 1988). However, the limited number of taxa in the HEC was by design. The collection intentionally represents fewer taxa, but with great detail for those included taxa. In some cases, over 200 embryos were used to represent the development of a single species. Wherever possible, the collection also included three "normal" examples at each stage to provide transverse, frontal, and sagittal preparations of that stage.

The HEC quickly became an international center of embryological research as the collection grew and was widely recognized as a valuable resource, encouraging both research and collaboration (Minot, 1905; Mall, 1913). Minot actively advertised the collection to researchers well into the last year of his life (Minot, 1914) and at that point at least 22 different authors had published on the basis of materials in the collection (Williston, 2010).

The HEC also became a model for documenting embryological research. For example, Minot applied the concepts of vouchering he learned from the zoological museums. Minot's collection-use policy requested that researchers cite HEC specimen numbers in publication (Minot, 1905). He

TABLE 1. SYSTEMATIC DIVERSITY OF HEC SPECIMENS ARRANGED BY CLASS. NAMES IN SECOND COLUMN REFLECT ORIGINAL TAXONOMY USED IN THE COLLECTION. IN SOME CASES ONLY COMMON NAMES WERE RECORDED IN THE COLLECTION. COLUMN TWO INCLUDES THE AUTHOR'S INTERPRETATIONS OF THE ORIGINAL SPECIES NAMES BASED ON MODERN TAXONOMY. COLUMN THREE PRESENTS A COMMON NAME INTERPRETATION OF EACH SPECIES.

Higher Classification	Taxonomy Used in HEC	Modern Interpretation of Taxonomy	Common Name	No. Series
Cephalochordate	*Amphioxus lanceolatus*	*Branchiostoma lanceolatum*	lancelet	14
Cyclostomata	*Bdellostoma stouti*	*Eptatretus stoutii*	Pacific hagfish	77
Cyclostomata	*Petromyzon planeri*	*Lampetra planeri*	European brook lamprey	46
Cyclostomata	*Petromyzon fluviatilis*	*Lampetra fluviatilis*	European river lamprey	42
Elasmobranchii	*Mustelus laevis*	*Mustelus mustelus*	smooth-hound shark	6
Elasmobranchii	*Raja clavata*	*Raja clavata*	thornback ray	1
Elasmobranchii	*Scyllium canicula*	*Scyliorhinus canicula*	small-spotted catshark	4
Elasmobranchii	*Squalus sucklii*	*Squalus suckleyi*	spotted spiny dogfish	1
Elasmobranchii	*Squalus acanthias*	*Squalus acanthias*	spiny dogfish	125
Elasmobranchii	*Torpedo ocellata*	*Torpedo torpedo*	eyed electric ray	92
Elasmobranchii	*Torpedo marmorata*	*Torpedo marmorata*	marbled electric ray	10
Actinopterygii	*Alosa sapidissima*	*Alosa sapidissima*	American shad	1
Actinopterygii	*Amia calva*	*Amia calva*	bowfin	56
Actinopterygii	*Batrachus tau*	*Opsanus beta*	gulf toadfish	37
Actinopterygii	*Ictalurus amiurus*	*Ameiurus nebulosus*?	brown bullhead	12
Actinopterygii	*Lepisosteus ossens*	*Lepisosteus ossens*	longnose gar	40
Actinopterygii	*Salvelinus fontinalis*	*Salvelinus fontinalis*	brook trout	45
Amphibia	*Ambystoma maculatus*	*Ambystoma maculatum*	spotted salamander	51
Amphibia	*Ambystoma tigrinum*	*Ambystoma tigrinum*	tiger salamander	81
Amphibia	*Bufo lentignosus*	*Anaxyrus americanus*?	American toad?	103
Amphibia	*Necturus maculatus*	*Necturus maculosus*	mud puppy	53
Amphibia	*Rana virescens*	*Lithobates sphenocephalus*?	leopard frog	36
Reptilia	*Alligator missisippiensis*	*Alligator missisippiensis*	American alligator	11
Reptilia	*Aristelliger praesiguis*	*Aristelliger praesignis*	Jamaican croaking lizard	33
Reptilia	*Chelydra serpentina*	*Chelydra serpentine*	common snapping turtle	7
Reptilia	*Chrysemys marginata*	*Chrysemys picta marginata*	painted turtle	165
Reptilia	*Crocodilus acutus*	*Crocodylus acutus*	American crocodile	1
Reptilia	*Eutania radix*	*Thamnophis radix*	Plains garter snake	78
Reptilia	*Eutania sirtalis*	*Thamnophis sirtalis*	common garter snake	24
Reptilia	*Iguana punctata*	*Iguana iguana* [?]	common green iguana?	2
Reptilia	*Iguana tuberculata*	*Iguana iguana*	common green iguana	3
Reptilia	*Lacerta agilis*	*Lacerta agilis*	sand lizard	13
Reptilia	*Lacerta muralis*	*Podarcis muralis*	common wall lizard	59
Reptilia	*Lacerta viviparta*	*Lacerta vivipara*	viviparous lizard	6
Reptilia	*Lygosoma weekesae*	*Pseudemoia spenceri*	Spencer's window-eyed skink	1
Reptilia	*Oxybalus sp.*	*Oxybelis* sp.[?]	vine snake?	3
Reptilia	*Sphenodon punctatus*	*Sphenodon punctatus*	tuatara	5
Reptilia	*Spherodactylus argus*	*Sphaerodactylus argus*	ocellated gecko	2
Aves	*Anas domestica*	*Anas platyrhynchos domesticus*	domestic duck	27
Aves	*Bonasa umbillicus*	*Bonasa umbellus*	ruffed grouse	17
Aves	"chick"	*Gallus gallus domesticus*	chicken	231
Aves	*Larus atricilla*	*Larus atricilla*	laughing gull	4
Aves	*Sterna hirundo*	*Sterna hirundo*	common tern	20
Aves	*Struthio sp.*	*Struthio* sp.	ostrich	12
Mammalia	"albino rat"	*Rattus norvegicus*	Norway rat	81
Mammalia	*Bradypus griseus*	*Bradypus variegatus*	brown-throated sloth	2

Table 1. Continued.

Higher Classification	Taxonomy Used in HEC	Modern Interpretation of Taxonomy	Common Name	No. Series
Mammalia	*Caluromys philander*	*Caluromys philander*	bare-tailed woolly opossum	3
Mammalia	"cat"	*Felis catus*	domestic cat	61
Mammalia	"guinea pig"	*Cavia cobaya*	guinea pig	22
Mammalia	*Cervus capreolus*	*Cervus capreolus*	roe deer	7
Mammalia	*Choerophon plicatus*	*Chaerephon plicata*	wrinkle-lipped free-tailed bat	1
Mammalia	"cow"	*Bos taurus*	cow	3
Mammalia	*Didelphys virginiana*	*Didelphis virginiana*	Virginia opossum	21
Mammalia	"dog"	*Canis domesticus*	domestic dog	5
Mammalia	*Lasiurus borealis*	*Lasiurus borealis*	red bat	5
Mammalia	**"man"	*Homo sapiens*	human	112
Mammalia	*Mus musculus*	*Mus musculus*	house mouse	52
Mammalia	*Oedipomidas geoffroi*	*Saguinus geoffroyi*	Geoffroy's tamarin	4
Mammalia	"pig"	*Sus scrofa domesticus*	domestic pig	148
Mammalia	"rabbit"	*Lepus canicula*	domestic rabbit	126
Mammalia	"sheep"	*Ovis aries*	sheep	72

**Human specimens deaccessioned; see text. Original identifications have not been confirmed.

considered such vouchering realistic as his slides were prepared according to archival standards and as a result would be "entirely in good condition after 30 years and probably after 100 years" (Minot 1900). Minot noted that, "no investigator will work less accurately because he knows that his specimens may be restudied by his successors" (Minot, 1905). Owing to these standards, today it is relatively easy to track published anatomical descriptions from HEC specimens back to their original histological sections. To date, at least 82 publications have cited HEC specimens (Appendix 1). Several of these publications are seminal works in comparative embryology, including two volumes of Franz Keibel's (1897–1938) landmark series Normentafeln zur Entwicklungsgeschichte der Wirbeltiere: *Lepus cuniculus* (Minot and Taylor, 1905) and *Squalus acanthias* (Scammon 1911). These two HEC-based volumes of the normal tables are notable for their meticulous citation of vouchered HEC specimens. Other notable publications include the early investigations on development of the hagfish, *Eptatretus stouti* (Dean, 1898, 1899; Conel, 1929, 1931, 1942). The HEC specimens used for these works are recognized as having been the only known hagfish embryo specimens in the 20th century (Gorbman, 1983; Gorbman and Tamarin, 1985; Wicht and Northcutt, 1995), although hagfish embryos have more recently been successfully laboratory reared (Ota *et al.*, 2007).

Production of new slide series and the use of the HEC slowed dramatically after Minot's death in 1915. Collection growth virtually stopped by the 1930s when researchers shifted emphases toward experimental embryology and the outbreak of World War I interrupted international collaboration (Hopwood, 2005). The collection fell into disuse, but was preserved at the Harvard Medical School's Warren Anatomical Museum (WAM), where it remained obscure for most of the 20th century.

Interest in the HEC slides re-emerged in the 1970s, and the collection was inventoried (Anonymous, 1976). The unique hagfish slides were rediscovered and again used in research (Gorbman, 1983; Gorbman and Tamarin, 1985). In 1992, the nonhuman embryos from the HEC were transferred

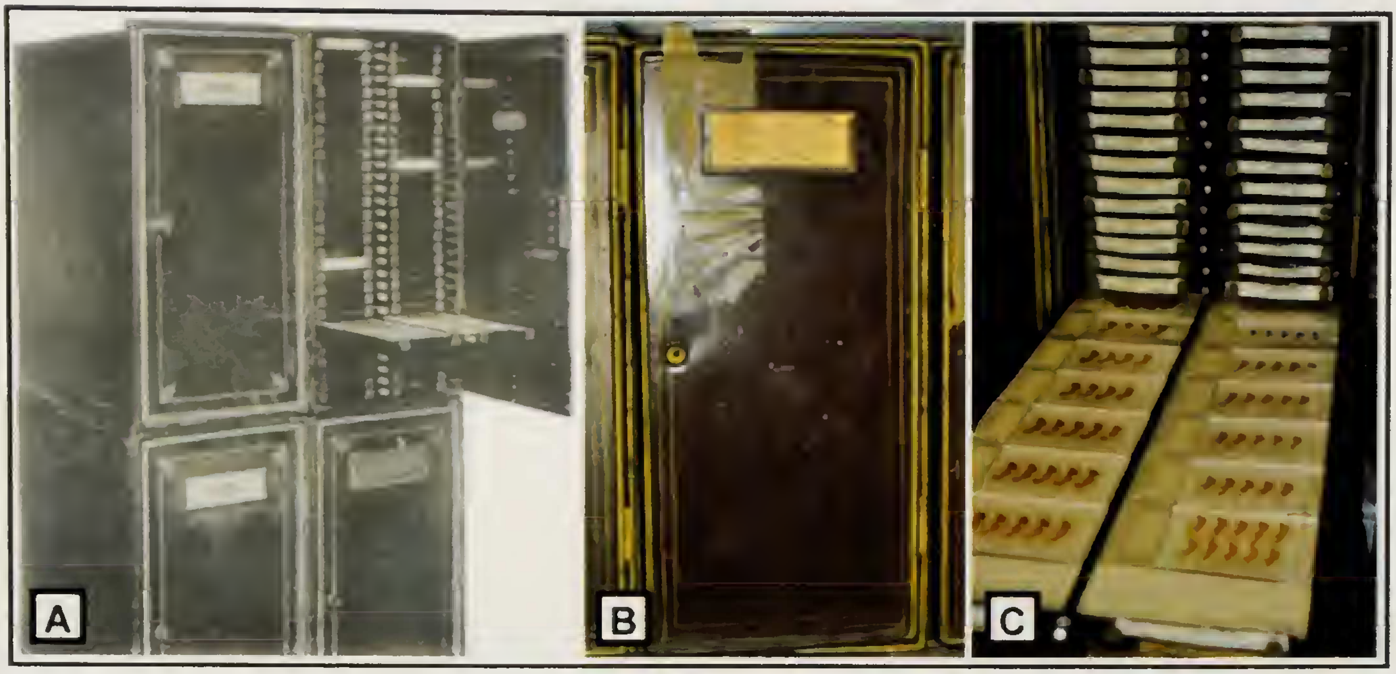

Figure 2. Tin slide cabinets from HEC. A, original photograph of tin cabinets from Minot (1905). B, C, photos of same-style cabinet in 2010.

from the Medical School to the MCZ, which is ironically the path opposite to the one Charles Minot himself took more than 100 years earlier. Also in 1992, the HEC human specimens were transferred from the WAM to the Carnegie Embryo Collection at the National Museum of Health and Medicine (NMHM) in Washington, District of Columbia, where they are still held as part of the Carnegie Collection (E. Lockett, personal communication).

In 2010 the contents and condition of the collection were reviewed (Williston, 2010). The collection was found to be in good condition and is still stored much as it had been in Minot's era, including the same organizational system and in many of the original slide cabinets (Fig. 2). Review of the slides (Williston, 2010) showed that the most common forms of damage over time were glass scratching and loose labels. The majority of slides were stained with alum cochineal, often with eosin counterstain, although over 40 combinations of stains are used, most notably iron hematoxylin and eosin. This staining has been relatively well preserved for most cases. The mountant used in the collection is dammar varnish and it is minimally yellowed. Where yellowing occurred it was typically limited to the coverslip edges.

Slides were found to have precise labeling with ample data that include taxa, specimen size, fixation, staining, and sectioning thickness. A unique catalog number organized all slide series, and slides within the series are individually lettered alphabetically to preserve the sequence of slides. In many cases there are photos or drawings of the original specimen before sectioning (Figs. 3, 4). Original drawings and figures are currently kept along with the original catalog records at the MCZ. The original card catalog (Anonymous, 1886–1974) also indicates that there were at one time stereoscopic photos, although these have yet to be found at the Medical School and are likely lost.

FUTURE FOR THE HEC

The HEC remains an archive for the foundational embryological research of the

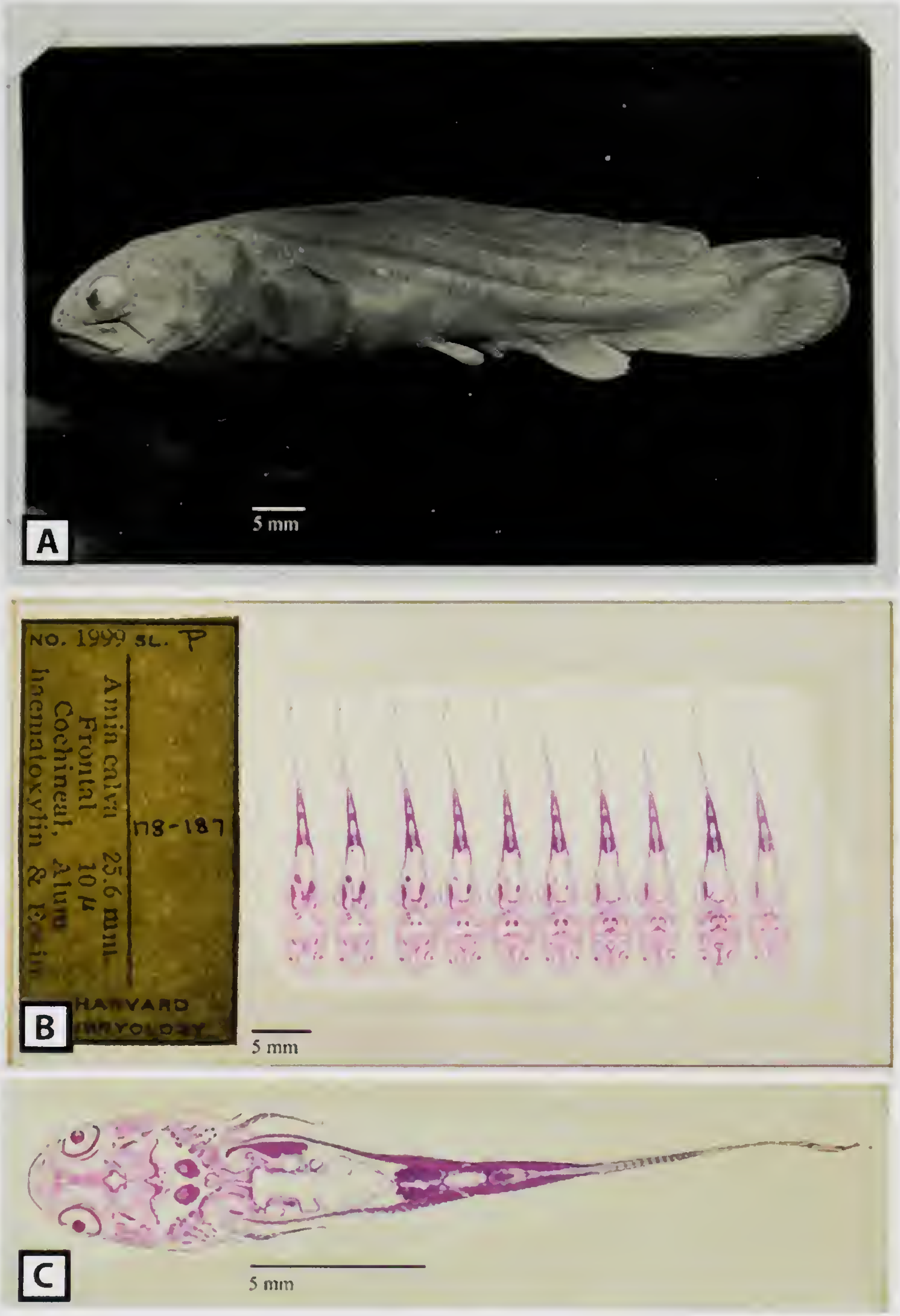

Figure 3. A, original photograph of HEC 1999, *Amia calva* specimen, before sectioning. B, image of slide P from specimen in A, slide P, *Amia calva*: serial sections 178–187. C, detail of section 179 from slide in B.

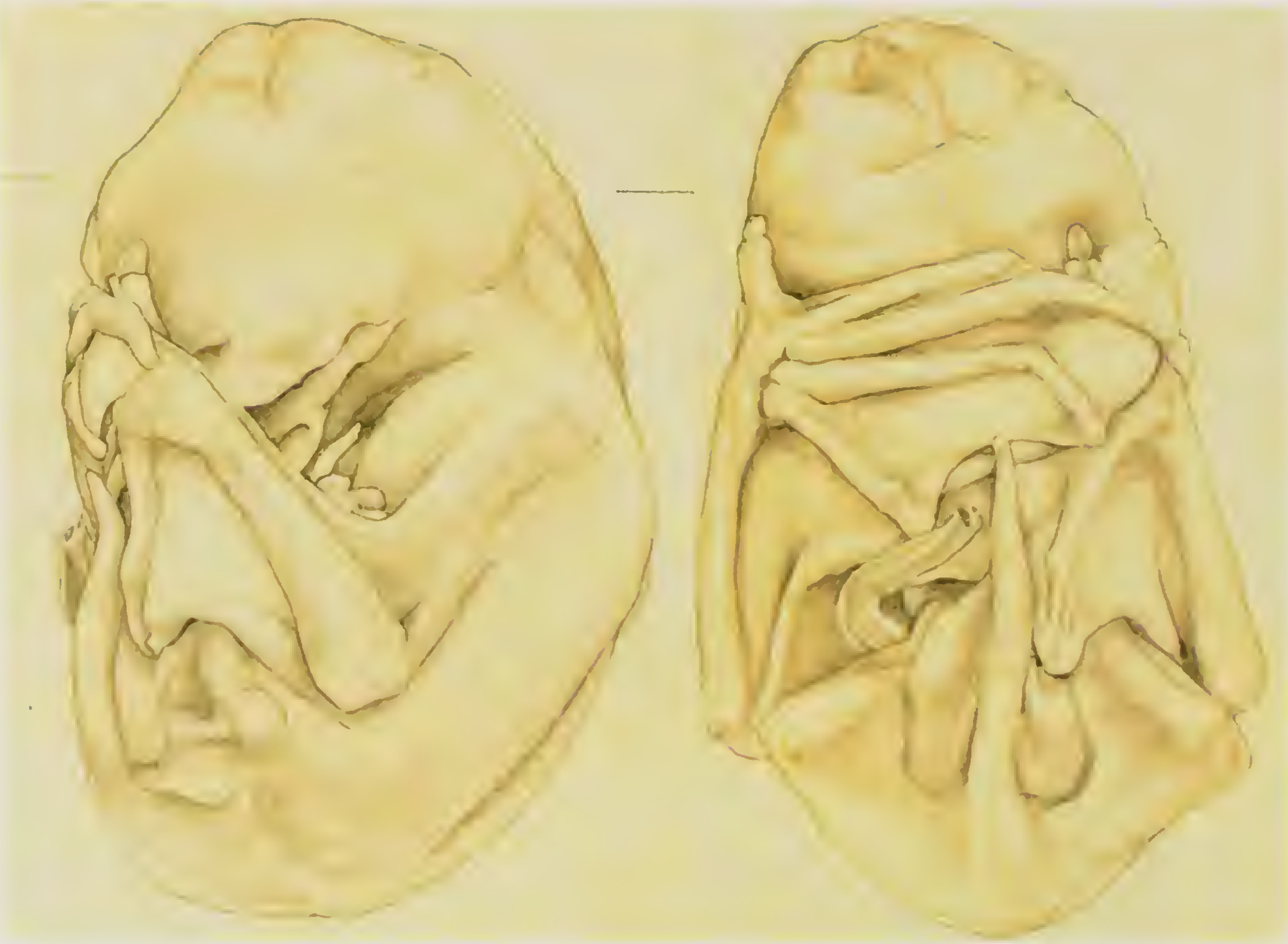

Figure 4. Original drawing of HEC 1606, free tail bat, before sectioning. Specimen represented was recorded as being 13.4 mm. Horizontal lines on the left side of each drawing represent the intended transverse sectioning plane.

early 20th century. The collection continues to serve as vouchers for this work and the bibliography of publications citing the collection demonstrates this value (Appendix 1). The complete documentation and the good condition of the collection offer historians the opportunity to examine the practices of the early 20th century. Additionally, the HEC offers perspective and insight on the legacy of Charles Sedgewick Minot, one of the most prominent and influential American embryologists of his time.

The HEC is also an irreplaceable resource for modern comparative embryology research. The systematic breadth and depth of the HEC make the collection suitable for a wide range of studies. Assembling this type of diversity in a single collection in today's world would be difficult or impossible. Some of the represented taxa are nearly impossible to collect today. For instance, Pacific hagfish (*E. stouti*) embryos continue to be rare, and the tuatara (*Sphenodon punctatus*) is critically endangered. Many more of the extensive collections of specimens collected in the wild such as spiny dogfish (*Squalus acanthias*) would simply be impractical to collect and prepare.

Researchers today are still making use of the HEC (Claeson, 2011; Miyashita, 2015; Sanger *et al.*, 2015). Additionally, new opportunities exist for using the collection as imaging and digitization of slide collections will offer new possibilities for accessing and utilizing slides and slide collections such as the HEC. Today's high-resolution scans have begun to rival the basic magnification available in many common compound microscopes. Digital image color profiles can be changed to digitally restain sections in some cases. Scans of histological slides can be archived and disseminated through the web, making the collection highly available for use.

The slides have potentially even more relevance and broader utility to modern researchers as digitized sections can now be reconstructed in 3D, essentially reinventing the wax-plate modeling technique used in the early 20th century, which stacked individual wax reproductions of serial sections to create 3D models (Hopwood 1999). Today, 3D visualization software can do similar modeling by compiling series of digital images and aligning and reassembling the individual sections into fully manipulative digital 3D models (e.g., Handschuh *et al.*, 2010). There has been great initial success in reconstructing parts of the tuatara series (Sanger *et al.*, 2015). The additional ability to share and manipulate 3D models in formats such as. pdf (Ruthensteiner and Hess, 2008) could expand the accessibility of the HEC for both collaborative research and teaching. Charles Minot's 19th-century foresight in archival collection building has not only allowed his collection to survive, it has also created a promising resource for 21st-century research. Recognizing this resource, the MCZ has recently undertaken a museum-wide effort to ensure the continued preservation and availability of the HEC for current and future researchers. Charles Minot's (1900) prediction that the HEC would last "probably after 100 years" has been exceeded and the legacy of the man and his vision of a well-vouchered embryology collection will continue probably after 100 years more.

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APPENDIX 1. PRELIMINARY LIST OF WORKS CITING THE HEC.

Allis, E. P. 1903. On certain features of the cranial anatomy of *Bdellostoma dombeyi*. *Anatomischer Anzeiger* **23**: 259–281, 321–339.

Atkinson, R. T. 1901. The early development of the circulation in the suprarenal of the rabbit. *Anatomischer Anzeiger* **19**: 610.

Baumgartner, E. A. 1915. The development of the hypophysis of *Squalus acanthias*. *Journal of Morphology* **26**: 391–446.

Baumgartner, E. A. 1916. On the development of the hypophysis in reptiles. *Journal of Morphology* **28**: 209–275.

Begg, A. S. 1912. The anomalous persistence in embryos of parts of the peri-intestinal rings formed by the vitelline veins. *American Journal of Anatomy* **13**: 103–110.

Boyden, E. A. 1922. The development of the cloaca in birds, with special reference to the origin of the

bursa of Fabricius, the formation of a urodeal sinus, and the regular occurrence of a cloaca fenestrae. *American Journal of Anatomy* **30:** 163–202.

Boyden, E. A. 1922. The early development of the cloaca in ostrich embryos, with special reference to the reduction of the caudal intestine. *Anatomical Record* **24:** 210–221.

Bremer, J. L. 1902. On the origin of the pulmonary arteries in mammals. *Journal of Anatomy* **1:** 137–144.

Bremer, J. L. 1904. On the lung of the opossum. *American Journal of Anatomy* **3:** 63–73.

Bremer, J. L. 1908. Aberrant roots and branches of the abducent and hypoglossal nerves. *Journal of Comparative Neurology and Psychology* **18:** 619–639.

Bremer, J. L. 1909. II. On the origin of the pulmonary arteries in mammals. *Anatomical Record* **1:** 137–144.

Bremer, J. L. 1912. The development of the aorta and aortic arches in rabbits. *American Journal of Anatomy* **13:** 111–128.

Bremer, J. L. 1932. Accessory bronchi in embryos; their occurrence and probable fate. *Anatomical Record* **54:** 361–374.

Butler, E. G. 1927. The relative role played by the embryonic veins in the development of the mammalian vena cava posterior. *American Journal of Anatomy* **39:** 267–353.

Camp, W. E. 1916. The development of the suprapericardial (postbranchial, ultimobranchial) body in *Squalus acanthias. Journal of Morphology* **28:** 369–415.

Cheng, C.-C. 1955. The development of the shoulder region of the opossum, *Didelphys virginiana*, with special reference to the musculature. *Journal of Morphology* **97:** 415–471.

Conel, J. L. 1929. The development of the brain of *Bdellostoma stouti.* I. External growth changes. *Journal of Comparative Neurology* **47:** 343–403.

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Dean B. 1899. *On the Embryology of Bdellostoma stouti: A General Account of Myxinoid Development from the Egg and Segmentation to Hatching.* Jena, Germany, Verlag von Gustav Fischer.

Dexter, F. 1895. Ein Beitrag zur Morphologie des verlängerten markes beim Kaninchen. *Archiv für Anatomie Und Entwicklungsgeschichte* **1895**: 423–437.

Dexter, F. 1899. Uber die Morphologie des Verdaunngssystem bei der Katze. *Archiv für Anatomie Und Entwicklungsgeschichte* **23:** 159–192.

Dexter, F. 1900. Additional observations on the morphology of the digestive tract of the cat. *Journal of the Boston Society of Medical Science* **4**(8): 205–212.

Dexter, F. 1902. The development of the paraphysis in the common fowl. *American Journal of Anatomy* **2:** 13–24.

Dexter, F. 1902. On the vitelline vein of the cat. *American Journal of Anatomy* **1:** 261–267.

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Escleshymer, A. C. 1904. The cytoplasmic and nuclear changes in the striated muscle cell of *Necturus. American Journal of Anatomy* **3:** 285–310.

Evans, H. M. 1909. On the earliest blood vessels in the anterior limb buds of birds and their relation to the primary subclavian artery. *American Journal of Anatomy* **9:** 281–319.

Fox, H. 1908. The pharyngeal pouches and their derivatives in the Mammalia. *American Journal of Anatomy* **8:** 187–250.

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Hoskins, E. R. 1916. On the development of the digitiform gland and the post-valvular segment of the intestine in *Squalus acanthias. Journal of Morphology* **28:** 329–367.

Huntington, G. S., and C. F. McClure. 1910. The anatomy and development of the jugular lymph sacs in the domestic cat (*Felis domestica*). *American Journal of Anatomy* **10:** 177–312.

Lewis, F. T. 1902. The development of the vena cava inferior. *American Journal of Anatomy* **1:** 229–244.

Lewis, F. T. 1903. The gross anatomy of a 12 mm pig. *American Journal of Anatomy* **2:** 211–225.

Lewis, F. T. 1904. The question of sinusoids. *Anatomischer Anzeiger* **25:** 211–226.

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